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The involvement of left inferior frontal and middle temporal cortices in word production unveiled by greater facilitation effects following brain damage

Grégoire Python[a,b,*], Bertrand Glize[c,d], Marina Laganaro[a]

[a] Faculty of Psychology, University of Geneva, Switzerland
[b] Neurorehabilitation Unit, Department of Clinical Neurosciences, CHUV, Lausanne, Switzerland
[c] EA4136 Handicap Activity Cognition Health, University of Bordeaux, France
[d] Physical Medicine and Rehabilitation Department, CHU Bordeaux, France

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ABSTRACT

In stroke-induced aphasia, left hemispheric lesions generally disturb the word production network. The left inferior frontal gyrus (LIFG) and the left middle temporal gyrus (LMTG) are involved in word production, but their respective contribution remains ambiguous. Previous investigations have largely focused on semantic interference to gather information about word production. Here we assessed the sensitivity of twenty-five aphasic speakers with either LIFG or LMTG lesions and matched controls to both semantic *facilitation* and *interference* in word production using the picture-word (PWP) and the blocked-cyclic naming (BCNP) paradigms. In the PWP (Exp. 1), semantic facilitation was exaggerated in participants with LIFG damage as compared to age-matched controls. In the BCNP (Exp. 2), repetition priming on production speed was larger in participants with LMTG damage than in controls, without any decrease of semantic errors. In the light of the results in the PWP, the LIFG appears to be a necessary structure to shape semantic facilitation. It might play an important role in properly adjusting the lexical selection threshold within the word production network. The results in the BCNP suggest that the LMTG conveys semantic-to-lexical connections likely involved in repetition priming and in mapping concepts to their correct lexical label. As consequences, participants with LIFG lesions possibly rely more on strategic vs automatic processes to efficiently select lexical entries in semantically competitive contexts, whereas participants with LMTG might exploit residual semantic-to-lexical activation.

1. Introduction

Most aphasic speakers have difficulties to select the words in their mental lexicon as efficiently as before their stroke. In everyday speech, they often experience word-finding difficulties resulting in increased latencies or in the production of lexical errors. In models of unimpaired speech production, the selection of the intended word is influenced by at least three mechanisms (Howard et al., 2006): spreading activation between semantically related items, lexical competition between related words and repetition priming. More recent models (Abdel Rahman and Melinger, 2009) proposed that the trade-off between facilitatory (i.e. activation/priming) and inhibitory (i.e. competition) processes depends on the number of inter-related active competitors. Neuroanatomical reviews of language production in healthy (i.e. non-brain-damaged) speakers have inconsistently attributed lexical selection to frontal (Price, 2010) or to temporal regions (Indefrey, 2011). Recent findings rather indicate that word planning recruits almost simultaneously frontal and temporal regions (Strijkers et al., 2017), and that a distributed network is involved in lexical-semantic activation and selection (Riès et al., 2017). Low performance in picture naming seems particularly associated with damage to the left middle temporal gyrus (LMTG), suggesting a critical role of this region in word production (Baldo et al., 2013), while the controlled aspects of lexical retrieval/selection have been rather associated with frontal areas (Riès et al., 2016; Snyder et al., 2011), and particularly with the left inferior frontal gyrus (LIFG). However, which aspects of lexical-semantic retrieval are mediated by the LMTG and which aspects of lexical control depend on the LIFG remain controversial, partly because interpretations were mainly drawn from semantic interference in the very specific context of the blocked-cyclic naming paradigm (Belke, 2017).

To clarify the role of the LMTG and the LIFG in lexical selection in semantically competitive contexts, we investigated how aphasic

* Corresponding author at: Faculty of Psychology, University of Geneva, Switzerland.
E-mail address: gregoire.python@unige.ch (G. Python).

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individuals with lesions either in the LMTG or in the LIFG responded to semantic *facilitation* and to semantic *interference* in two paradigms known to induce both effects in healthy speakers, namely the picture-word interference and the blocked-cyclic naming paradigms.

1.1. Facilitation and interference in the Picture-Word Naming Paradigm

In the Picture-Word Interference task, a word is presented along with (simultaneously or in close vicinity to) a picture to name. The unrelated condition (usually a picture paired with a semantically and phonologically unrelated word, e.g. apple-bed) is compared to a semantic condition consisting of the same picture with a semantically related word (e.g. apple-banana). The typical and often described result is semantic interference, i.e. longer naming latencies in the context of semantically related words competing with the picture name in healthy speakers (Costa et al., 2005; Damian and Spalek, 2014; Finkbeiner and Caramazza, 2006; Hantsch et al., 2012, 2005; Kuipers et al., 2006; La Heij, 1988; La Heij and van den Hof, 1995; Lupker, 1979; Rosinski, 1977; Rosinski et al., 1975; Sailor et al., 2009; Starreveld and La Heij, 1996; Vitkovitch and Tyrrell, 1999) and increased error rates in persons with aphasia (Hashimoto and Thompson, 2010; Piai and Knight, 2017). Crucially, the Picture-Word "Interference" paradigm can also induce semantic facilitation under certain experimental conditions (see Mahon et al., 2007, for a review). To prevent ambiguities, we will refer to this task as the Picture-Word Paradigm (PWP) hereafter. In the PWP, the polarity of the effect (interference vs facilitation) can change depending on the Stimulus Onset Asynchrony (SOA): a near-to-0 SOA leads to semantic interference but negative SOAs, especially when longer than − 400 ms, usually causes semantic facilitation (Alario, 2001; Bloem et al., 2004; Glaser and Düngelhoff, 1984; Python et al., 2018; Zhang et al., 2016). The type of relation between the word and the picture can also influence the polarity of the effect, at least with a short SOA (Mahon et al., 2007): interference has been obtained with coordinate, subordinate and superordinate common nouns, but facilitation occurred with a larger panel of semantic relations (coordinate, subordinate, superordinate, associate, related adjective and related verb). In particular, within-subject dissociations were reported between associative relations (e.g. banana-monkey) inducing semantic facilitation or no behavioral effect, and coordinate relations (e.g. banana-apple) inducing semantic interference (Alario, 2001; Costa et al., 2005; Sailor et al., 2009; Wong et al., 2017). The PWP has been extensively used with healthy speakers to test and feed models of word production, whereas only very few studies investigated the effects of the PWP in aphasic speakers. And yet, it is of interest for aphasia research and rehabilitation to better understand the conditions facilitating or interfering with lexical selection when language brain networks are damaged. Hashimoto and Thompson (2010) reported increased error rates and RTs (i.e. interference) in a group of eleven non-fluent aphasic individuals and age-matched healthy speakers. However, the authors also observed that three participants showed the reverse pattern on RTs, namely semantic facilitation at SOAs − 300 ms or 0 ms, a pattern which was also reported in a case study by Wilshire et al. (2007) at a SOA of 0 ms. Another group study with six individuals presenting with left prefrontal cortical (LPFC) lesions (Piai et al., 2016) found no reliable semantic interference (SOA of 0 ms) and concluded that this region was not critical to resolve semantic interference in the PWP. More recently, Piai and Knight (2017) compared groups of participants with LPFC vs temporal lesions using the PWP (SOA of 0 ms). In the LPFC group, semantic interference was found only on errors, but in the group of participants with a temporal lesion, semantic interference was found both on RTs and errors, with more semantic interference on accuracy than controls. The authors deduced that the temporal lobe was necessary for lexical activation and selection, whereas the role of the LPFC remained unclear.

1.2. Facilitation and interference in the Blocked-Cyclic Naming Paradigm

The Blocked Cyclic Naming Paradigm (BCNP; Damian et al., 2001) has also been used in many studies to investigate semantic context effects on single word production especially in healthy participants, but also in aphasic speakers. In this paradigm, naming performance is compared between two semantic contexts: within homogeneous blocks of stimuli from the same semantic category and within heterogeneous blocks of stimuli from different semantic categories. The repetition of the same pictures in successive cycles for each type of block is a core feature of this paradigm and necessary for semantic interference to arise. At the same time, the iteration of the same pictures in the BCNP also facilitates word production from the second cycle in both types of blocks, even though repetition priming is larger in heterogeneous vs homogeneous blocks (Navarrete et al., 2014). In healthy subjects, semantic facilitation on naming latencies is typically observed in the first presentation cycle (Abdel Rahman and Melinger, 2007; Crowther and Martin, 2014; Schnur et al., 2006), whereas stable semantic interference is seen afterwards (Belke and Stielow, 2013). In aphasic speakers, the BCNP served to investigate the neuroanatomical correlates of word production and the underlying mechanisms of anomia. Schnur and colleagues tested eighteen individuals with the BCNP (Schnur, 2004; Schnur et al., 2006, 2009, 2005) and found semantic interference on naming accuracy especially at later cycles in participants with Broca aphasia and on RTs in participants with other types of aphasia (NonBroca). Semantic interference effects on accuracy were larger in participants with a temporal (vs frontal) lesion, but participants with a damaged left inferior frontal gyrus (LIFG) showed a linear increase of errors (independently of the overall magnitude of semantic interference) over the cycles. The authors concluded in favor of a deficient selection mechanism in the Broca/LIFG group, that struggled to overcome the activation of semantically related words. Harvey and Schnur (2015) also found in fifteen aphasic speakers that the amount of semantic interference on accuracy correlated with damage in posterior temporal regions, whereas the linear increase of semantic interference tended to be related to the LIFG. Finally, Riès et al. (2015) reported more semantic interference on accuracy in participants with a LPFC lesion, when comparing them to participants with a contralateral lesion and age-matched controls. This differential pattern was interpreted as increased difficulty in overcoming lexical competition in the LPFC group, due to a cognitive control mechanism relying on the LPFC. Several case studies using the BCNP also reported semantic interference in aphasic individuals with frontal or unspecified lesions in terms of naming accuracy (McCarthy and Kartsounis, 2000; Wilshire and McCarthy, 2002; Hodgson et al., 2003; Schwartz and Hodgson, 2002; Scott and Wilshire, 2010) or naming latencies (Biegler et al., 2008). These case reports generally merged the participant's results over the cycles, even if interference materialized only in later cycles.

1.3. Scope of the present study

So far, PWP and BCNP studies on aphasic speakers following stroke focused on semantic *interference*. In contrast, *facilitation* effects (i.e. semantic facilitation or repetition priming), which may convey insightful information on word production to the same extent as interference, were not investigated or were incidentally observed. In particular, in the BCNP, the first facilitative cycle was commonly discarded from the analyses (see Ries et al., 2014; Riès et al., 2015) thus also restricting the potential analysis of repetition priming, and in the PWP close-to-0 SOAs and categorical primes were usually tested, i.e. conditions known to generate semantic interference but no facilitation. The aim of the current study was to investigate both semantic *facilitation* and *interference* in two groups of fluent aphasic speakers by means of the PWP with different SOAs and with categorical and associative primes (Experiment 1; 12 aphasic individuals and 12 controls), and of

Table 1
Demographic, lesion and behavioral data of the 12 aphasic persons in Experiment 1.

	Participant	Gender	Age	Lesion size	Auditory lexical comprehension BDAE	PPTT – 3 written words version
Damaged LIFG	1	male	55	17.08	NA	NA
	2	male	75	60.42	97%	96%
	3	female	79	14.05	100%	90%
	4	male	70	39.03	100%	94%
	5	male	66	14.02	100%	96%
	6	male	67	29.02	100%	87%
	Mean		*69*	*28.94*	*99%*	*93%*
Damaged LMTG	7	male	62	22.18	100%	90%
	8	male	63	37.61	97%	90%
	9	female	23	76.74	100%	92%
	10	male	40	24.48	100%	88%
	11	male	69	17.8	NA	87%
	12	female	54	20.74	NA	98%
	Mean		*52*	*33.26*	*99%*	*91%*
	p		*.14*	*.74*	*.42*	*.70*

Damaged LIFG = participants with brain damage encompassing the left inferior frontal gyrus but sparing the left middle temporal gyrus; Damaged LMTG = participants with brain damage encompassing the left middle temporal gyrus but sparing the left inferior frontal gyrus; Lesion size is given in cubic centimeter; Auditory lexical comprehension BDAE = accuracy at the word discrimination subtest of the Boston Diagnostic Aphasia Evaluation (n = 72), PPTT = accuracy at the Pyramids and Palm Trees Test – 3 written words version (n = 52); Means are provided for each subgroup and p-values (Student's *t*-tests) attest that there is no significant difference between the subgroups.

the BCNP including an analysis of the first (facilitative) cycle and of the repetition priming across cycles (Experiment 2; 13 aphasic individuals and 13 controls). In order to shed light on the respective contributions of the LMTG and the LIFG to word production, we compared control participants without brain lesion to aphasic individuals with a lesion encompassing the LMTG (without LIFG damage) or a lesion encompassing the LIFG (without LMTG damage).

2. Experiment 1

The first experiment consisted of picture naming under the influence of previously presented words (PWP), also referred to as an "explicit priming paradigm" (Levelt et al., 1999). It was run either with a short SOA and a single written word prime ("standard PWP type" hereafter) or with a long SOA and one or two auditory words preceding the picture in order to maximize facilitation effects ("facilitative PWP type" hereafter). Different pictures were used for each PWP type and all participants began with the standard PWP type.

2.1. Methods

2.1.1. Participants

Eighteen aphasic persons took part in this experiment, but six of them were excluded because they presented lesions encompassing both the LIFG and the LMTG, or neither area (see Table 1 for the remaining twelve participants). They were recruited in Lausanne (Switzerland) or in Bordeaux University Hospital as part of a larger study and gave written informed consent, which was validated by local ethical research committees[1] in accordance with the Declaration of Helsinki. They were included if they were French-speaking, right-handed, suffered a first episode of left hemispheric stroke and classified as "aphasic" according to a language screening assessment in the first days after stroke (Flamand-Roze et al., 2011), without prior dementia or psychiatric diseases. All participants were tested 24–32 months after their stroke, that remained the sole neurologic event at the date of testing. The participants had mild anomia (> 90% accuracy) as assessed by the French version of the Boston Diagnostic Aphasia Evaluation (BDAE; Mazaux and Orgogozo, 1982). They showed spared to mildly impaired auditory word comprehension (BDAE, see Table 1) and lexical-semantic knowledge for written words as assessed by the Pyramids and Palm Trees Test (Howard and Patterson, 1992, see Table 1).

In addition, twelve French-speaking and right-handed participants without history of neurological or psychiatric disorder also performed the experiment. This group of unimpaired controls was matched to the group of aphasic participants in terms of sex (three females), age (mean 61 y.o., range 45–79) and years of education (mean 13.5 years vs 12.3 years for the brain-damaged group (p = .37)).

2.1.2. Lesion analysis

All participants underwent clinical brain magnetic resonance imaging (MRI) during their hospitalization in the stroke unit of the Bordeaux University Hospital or in Lausanne University Hospital, except for two participants who underwent computerized tomography (CT) scan. The lesion mapping was conducted on axial diffusion-weighted images acquired in the acute phase (or T2*-weighted images in case of intra-cerebral haemorrhage) that were imported with the software MRIcro.[2] Lesions were drawn manually as regions of interest by a trained neurologist masked from the behavioral results and images were normalized to a standard brain template from the Montreal Neurological Institute, using rigid and elastic deformation tools provided in the software package Statistical Parametric Mapping.[3] Deformations were applied to the whole brain except for the voxels contained in the lesion mask in order to avoid deformation of the lesioned tissue (Brett et al., 2001; Volle et al., 2008). After non-linear normalization, the lesions were analyzed in terms overlaps with MRIcro and MRIcron[4] softwares. They were separated in two groups according to the presence of a lesion in the inferior frontal gyrus vs in the middle temporal gyrus (Fig. 1). The two subgroups of six participants were comparable in terms of age, lesion size and behavioral measures of word comprehension (Table 1).

2.1.3. Material and procedure

Fifty-six black and white line drawings with a high name agreement in French (> 70%) were carefully selected in two databases (Alario and

[1] CPP-SOOM3, University of Bordeaux and CER of Canton de Vaud in Switzerland.

[2] http://www.mricro.com; Version 6 June 2013; Chris Rorden, Columbia, SC, USA.

[3] http://www.fil.ion.ucl.ac.uk/spm; SPM8.

[4] http://www.mccauslandcenter.sc.edu/mricro/mricron/; Chris Rorden, Columbia, SC, USA.

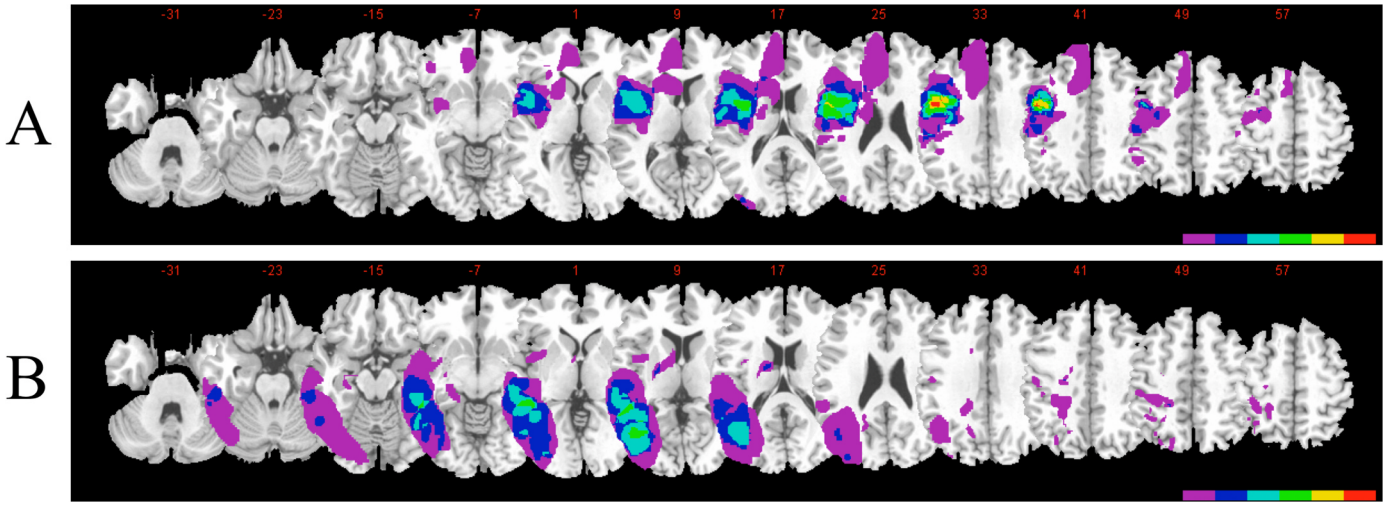

Fig. 1. A. Lesion overlap for the subgroup of six participants with damaged LIFG and spared LMTG; B. Lesion overlap for the subgroup of six participants with damaged LMTG and spared LIFG.

Ferrand, 1999; Bonin et al., 2003). Each picture was matched with one or two associative word/s from a different semantic category (e.g. bike-wheel) (Ferrand and Alario, 1998), one or two word/s from the same semantic category (e.g. bike-scooter) (Bueno and Megherbi, 2009) and one or two unrelated word/s taken from the set of associative and categorical words independently of the PWP type (e.g. bike-ant). The verbs were modified into their corresponding common nouns (e.g. to fly – flight). No initial or final phoneme was shared between the prime and the target. The exhaustive list of stimuli can be found in Supplementary Table S1.

The fifty-six pictures were divided into two sets: thirty-five pictures were used in a "standard PWP type" (short SOA condition with a single prime) and twenty-one pictures in a "facilitative PWP type" (long SOA condition with multiple primes). The two sets of stimuli were matched on lexical frequency and word length (number of phonemes), and both sets covered at least twelve different semantic categories.

The experiment began with the standard PWP type, in which the thirty-five pictures used were presented three times: after an associative, a categorical and an unrelated word. The order of presentation was pseudo-randomized with maximum two consecutive trials from the same semantic condition and each presentation of the picture separated by at least ten other pictures, for a total of 105 naming trials (35 pictures × 3 conditions). Each of the 105 trials began with a fixation cross of 1250 ms, then the written word was presented for 53 ms, the fixation cross for 13 ms and the target picture remained onscreen for 2000 ms. After these 105 trials, a break was provided.

In the facilitative PWP type, the twenty-one pictures used were preceded by one or two priming words presented auditorily, giving long negative SOAs, known to induce semantic facilitation. When two priming words were played, they were both categorically related, associatively related or not related to the picture. We have shown previously that providing two related words before the picture to name increased semantic facilitation effects but impacted the same word planning processes as a single prime (Python et al., 2018). The rationale for choosing auditory words and multiple cues was to get closer to clinical practice for semantic facilitation (i.e. aphasic participants being provided spoken help from speech and language therapists to retrieve words). Because the number of primes was not the focus of the current study, only the semantic condition (i.e. unrelated, associative, categorical) was retained as a main factor in the analyses. Each of the 126 trials (21 pictures × 3 conditions × 2 no. of primes) began with a fixation cross of 250 ms, then the word(s) was/were presented auditorily (with an interval of 150 ms in case of two words), and after a 150 ms fixation cross, the target picture was presented for 2000 ms. The SOA varied for each trial according to the word(s) length and was at least − 410 ms. Even if a unique SOA for each item might at first glance seem a sub-optimal procedure, it has been shown that semantic facilitation effects are stable between − 400 ms and − 1000 ms and not modulated by the SOA anymore (Zhang et al., 2016).

Aphasic persons sat comfortably next to a speech and language therapist trainee in front of a computer screen. They were first familiarized with all the pictures and the corresponding names. At their own pace, they could name the pictures once with the corresponding names written underneath, and once without the names. In case of errors during familiarization, immediate feedback was provided and the expected modal name was given for repetition. During the experiment, they were asked to name the pictures with a single name, as rapidly and exactly as possible and to ignore the words presented before the pictures. For each of the 231 naming probes, the next trial was launched by a mouse click by the experimenter, so that the timing was adapted to the participant and a break was possible at any time. Responses were recorded up to three seconds after the picture presentation by E-Prime 2.0 software[5] (Psychology Software Tools, Pittsburgh, PA).

2.1.4. Analyses

2.1.4.1. Error scoring and analysis. Responses were considered as errors when they did not correspond to the single target name presented during the familiarization and training phases. They were classified as semantic errors (e.g. "onion" for "leek"), phonological errors (e.g. "opion" for "onion"), omissions (no response given within 3000 ms), hesitations (a filled pause like "hum" was produced before the response), circumlocutions (a definition of the word was given), formal errors (e.g. "parrot" for "carrot") or unrelated errors (e.g. "donkey" for "leg"). Generalized mixed models for binomially distributed outcomes (Jaeger, 2008) were used to analyze the errors, with semantic condition, PWP type and group as fixed factors and random slopes for the semantic condition both by participants and by items. References were the non-brain-damaged control group, the unrelated condition and the standard PWP type (single written prime and short SOA). The main error type was analyzed with generalized mixed models with items and participants as random factors, but without random slopes due to the lack of convergence with random slopes. Models computed with the default Nelder-Mead optimization algorithm failed to converge, so that the Bound Optimization BY

[5] Psychology Software Tools, Inc. [E-Prime 2.0]. Retrieved from http://www.pstnet.com/.

Table 2
Mean RT (in ms) and error rate (in %) per condition and group for each PWP type.

		Controls (n = 12)		Damaged LIFG (n = 6)		Damaged LMTG (n = 6)	
		RTs	Errors	RTs	Errors	RTs	Errors
Standard PWP type	UNR	808	1.5%	963	1.9%	930	4.6%
	ASS	798	1.3%	968	2.0%	936	3.3%
	CAT	841	1.0%	967	2.6%	965	5.7%
Facilitative PWP type	UNR	754	1.1%	956	1.7%	866	2.0%
	ASS	699	0.4%	827	1.6%	806	2.6%
	CAT	701	0.8%	877	1.4%	809	2.6%

UNR = unrelated condition; ASS = associative condition; CAT = categorical condition; Standard PWP type = 105 stimuli with a short negative SOA and a single written word prime; Facilitative PWP type = 126 stimuli with a long negative SOA and with single or double auditory word prime/s.

Quadratics Approximation was used instead (Powell, 2009). The full analysis code is available in the Supplementary material.

2.1.4.2. RT extraction and analysis. The software Checkvocal (version 2.2.6, Protopapas, 2007) was used to manually determine the vocal onset of each correct response. Responses produced after 3000 ms were considered outliers. Naming latencies situated below or above three standard deviations of each subject's mean were excluded and RTs were log-transformed to resemble a normal distribution. Linear regression mixed-effects models (Baayen et al., 2008) with semantic condition, PWP type and group as fixed factors and random slopes for the semantic condition both by participants and by items were computed in the R software (R Development Core Team, 2003) with the lme4 (Bates et al., 2015) and lmerTest packages (Kuznetsova et al., 2017). The non-brain-damaged control group, the unrelated condition and the standard PWP type were again used as references.

2.2. Results

For the three groups, mean error rates and RTs in each condition and for each PWP type are presented in Table 2.

2.2.1. Accuracy

The mean error rate was 1.7% in the control group (range 0–6.3%), 6.5% in the LIFG group (3.0–16.3%) and 11.9% in the LMTG group (0–34.1%), leading to 6.2% of data exclusion due to errors (344 trials among the 5544 observations). Overall, the controls were significantly more accurate than the LIFG group ($p = .006$) and the LMTG group ($p = .002$), but no other single variable or interaction reached significance (see Table 3 for the full model). Errors were mainly hesitations (33%), omissions (26%), phonological errors (16%) and semantic errors (9%). The amount of hesitations (the main error type) was not modulated by the PWP type, the semantic conditions and the group (all z between -1.37 and 1.86, all $ps > .05$).

2.2.2. Naming latencies

The exclusion of RTs below/above three standard deviations of each subject's mean concerned 1.7% of responses (96 trials among the 5544 observations: 1.9% for the controls, 1.7% for the LIFG group and 1.5% for the LMTG group). Mean results per group and condition are reported in Table 2 and individual results in terms of proportion of RT differences between semantic conditions in Fig. 2.

On naming latencies (see Tables 2 and 3), the model yielded significant main effects of the PWP type ($F(1,54.4) = 113.189$, $p < .001$) with slower latencies in the standard PWP as compared to the facilitative PWP, of the group ($F(2,21) = 8.075$, $p = .003$) with participants without brain damage being overall faster than individuals with LIFG damage ($p = .002$) as well as LMTG damage ($p = .007$), and of the semantic condition ($F(2,37) = 13.517$, $p < .001$) with categorical primes increasing naming latencies as compared to unrelated primes ($p = .03$). There were significant interactions between the PWP type and the group ($F(2,4860.3) = 6.412$, $p = .002$), between the PWP type and the semantic condition ($F(2,62.4) = 24.723$, $p < .001$), and a triple interaction between the PWP type, the semantic condition and the group ($F(4,4864.8) = 3.814$, $p = .004$). The effects of associative and categorical primes (as compared to unrelated primes) were dependent of the PWP type ($ps < 0.001$). Crucially, only the performance of participants with LIFG damage (as compared to controls) was dependent of the PWP type ($p = .002$) in contrary to participants with LMTG damage. This was particularly salient for associative vs unrelated primes with a long SOA ($p = .002$; cf. significant triple interaction in Table 3), where semantic facilitation was descriptively larger for participants with LIFG lesions than for controls and with a short SOA. No other interaction reached significance.

Because the naming latencies of individuals with LIFG damage were dependent of the PWP type and this dependency differed from controls, further models were computed separately for each PWP type keeping only the LIFG group and the control group.[6] In order to evaluate the impact of presenting one vs two word(s) before the picture in the facilitative PWP, the model computed for this PWP type included the number of primes as fixed factor, alongside the group and the semantic condition (the references were the controls, the unrelated condition and a single word prime). Random slopes for the semantic condition by participants and by items were also included but not for the number of primes, due to the lack of convergence. In the facilitative PWP, LIFG participants were significantly slower than controls ($\beta = 0.241$, $SE = 0.053$, $t(19.8) = 4.523$, $p < .001$), semantic facilitation was observed in both semantic conditions (UNR vs ASS: $\beta = -0.040$, $SE = 0.016$, $t(2052) = -2.464$, $p = .01$; UNR vs CAT: $\beta = -0.059$, $SE = 0.016$, $t(2052) = -3.558$, $p < .001$), but the number of primes did not affect naming latencies ($t < 1$). Two interactions were significant. First, participants with LIFG lesions showed more semantic facilitation after associative primes (vs unrelated primes) than controls (interaction between LIFG vs controls and ASS vs UNR; $\beta = -0.070$, $SE = 0.029$, $t(2053) = -2.387$, $p = .017$). Second, naming latencies were shorter after two primes than one prime in the associative condition (interaction between the number of primes and ASS vs UNR; $\beta = -0.086$, $SE = 0.023$, $t(2052) = -3.705$, $p < .001$). Other two-way and three-way interactions were not significant (all $ps > .07$).

In the standard PWP type, individuals with damaged LIFG were overall slower than individuals without brain lesion ($\beta = 0.171$, $SE = 0.044$, $t(16.1) = 3.882$, $p = .001$). As compared to unrelated primes, naming latencies were longer after categorical primes ($\beta = 0.036$, $SE = 0.012$, $t(55.7) = 3.112$, $p = .003$) but not after associative primes ($\beta = -0.013$, $SE = 0.012$, $t(55.1) = -1.072$, $p = .29$). Despite no significant interaction ($ps > .08$), semantic interference on

[6] In order to correct the model for family-wise errors (FWE) due to multiple comparisons, results were considered significant only when $p \leq .017$ (i.e. $p < .05$ divided by three models conducted on RTs), according to the conservative Bonferroni correction procedure.

Table 3
Results of the inferential statistics for the error rates (top) and the naming latencies (bottom) in the PWP.

Effects on errors	β	SE	z	p
PWP type	− 0.075	0.720	− 0.105	0.916
LIFG vs controls	2.147	0.791	2.714	0.006
LMTG vs controls	2.448	0.784	3.123	0.002
ASS vs UNR	0.651	0.678	0.960	0.337
CAT vs UNR	− 0.007	0.746	− 0.010	0.992
PWP type : LIFG vs controls	− 0.319	0.798	− 0.400	0.689
PWP type : LMTG vs controls	− 1.334	0.786	− 1.696	0.090
PWP type : ASS vs UNR	− 1.501	1.077	− 1.393	0.164
PWP type : CAT vs UNR	− 0.304	0.993	− 0.306	0.760
LIFG vs controls : ASS vs UNR	− 0.887	0.775	− 1.145	0.252
LMTG vs controls : ASS vs UNR	− 0.870	0.742	− 1.172	0.241
LIFG vs controls : CAT vs UNR	0.284	0.820	0.347	0.729
LMTG vs controls : CAT vs UNR	0.319	0.800	0.398	0.690
PWP type : LIFG vs controls : ASS vs UNR	1.219	1.241	0.982	0.326
PWP type : LMTG vs controls : ASS vs UNR	2.022	1.189	1.700	0.089
PWP type : LIFG vs controls : CAT vs UNR	− 0.071	1.144	− 0.062	0.950
PWP type : LMTG vs controls : CAT vs UNR	0.158	1.128	0.140	0.889

Effects on naming latencies	β	SE	df	t	p
PWP type	− 0.074	0.017	93	− 4.370	< 0.001
LIFG vs controls	0.171	0.050	23	3.417	0.002
LMTG vs controls	0.149	0.050	24	2.981	0.007
ASS vs UNR	− 0.013	0.017	62	− 0.779	0.439
CAT vs UNR	0.037	0.017	72	2.213	0.030
PWP type : LIFG vs controls	0.063	0.021	486	3.030	0.002
PWP type : LMTG vs controls	− 0.014	0.021	486	− 0.670	0.503
PWP type : ASS vs UNR	− 0.070	0.020	117	− 3.511	< 0.001
PWP type : CAT vs UNR	− 0.116	0.021	100	− 5.391	< 0.001
LIFG vs controls : ASS vs UNR	0.013	0.026	53	0.493	0.624
LMTG vs controls : ASS vs UNR	0.116	0.027	57	0.433	0.667
LIFG vs controls : CAT vs UNR	− 0.030	0.025	61	− 1.199	0.235
LMTG vs controls : CAT vs UNR	0.006	0.026	68	0.220	0.826
PWP type : LIFG vs controls : ASS vs UNR	− 0.092	0.029	4858	− 3.137	0.002
PWP type: LMTG vs controls : ASS vs UNR	− 0.003	0.030	4863	− 0.102	0.918
PWP type : LIFG vs controls : CAT vs UNR	0.007	0.029	4860	0.238	0.812
PWP type : LMTG vs controls : CAT vs UNR	0.004	0.030	4873	0.149	0.882

PWP type = SOA duration, modality (written vs auditory) as well as number of words (one vs one or two) presented before the picture; LIFG = group of six participants with a lesion in the left inferior frontal gyrus; LMTG = group of six participants with a lesion in the left middle temporal gyrus; controls = control group of twelve unimpaired participants; ASS = associative word-picture relation; UNR = unrelated word-picture relation; CAT = categorical word-picture relation.

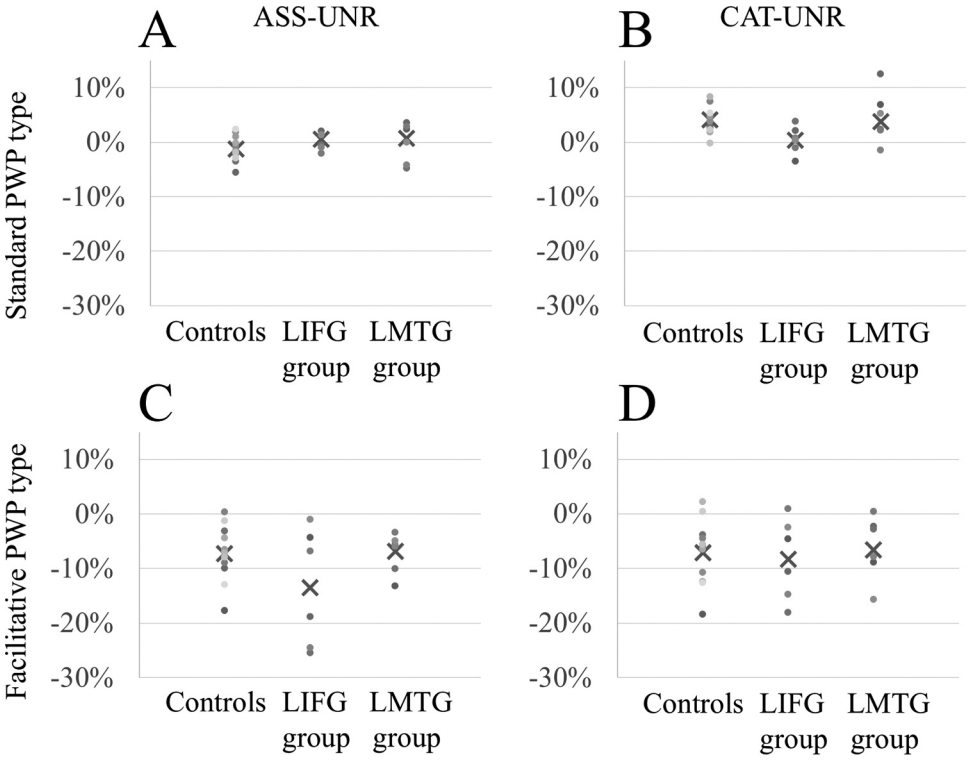

Fig. 2. Proportion of RT differences in each group of participants: A. between associative and unrelated conditions with the standard PWP type; B. between categorical and unrelated conditions with the standard PWP type; C. between associative and unrelated conditions with the facilitative PWP type; D. between categorical and unrelated conditions with the facilitative PWP type; crosses represent mean RT differences for each group and dots represent the individual data; negative values indicate facilitation, positive values semantic interference.

categorical primes was descriptively larger in controls (+ 33 ms) than in participants with LIFG lesions (+ 4 ms), as reported in previous PWP studies.

Finally, we checked whether the lesion size correlated with the differences between semantic conditions in terms of naming latencies or errors, which does not seem to be the case (all Spearman coefficients between -0.05 and 0.57, all ps > .05).

2.3. Discussion

2.3.1. Semantic facilitation amplification

Priming words presented with long negative SOAs induced semantic facilitation in all three groups, which is actually an ordinary pattern (Alario, 2001; Bloem et al., 2004; Python et al., 2018; Zhang et al., 2016). These results further confirm that not only associative relations but also categorical word-picture relations can facilitate speech production (Abel et al., 2012). Moreover, individuals with a LIFG lesion showed significantly larger semantic facilitation effects than controls and individuals with a LMTG lesion, suggesting that the LIFG might play a role in regulating the amount of semantic facilitation in the PWP.

2.3.2. The LIFG contribution

The LIFG seems important to let non-target words have an impact on the selection of the target word and different interpretations are possible to account for the exaggeration of semantic facilitation in participants with LIFG damage. On the one hand, the flow of activation could have been either abnormally fast/strong and overcoming lexical competition, which leads to increased facilitation (Abdel Rahman and Melinger, 2009; Chen and Mirman, 2012). On the other hand, lexical competition and more particularly lateral inhibition could have been weakened by a lesion to the LIFG (de Zubicaray and McMahon, 2009). Teasing apart these interpretations is beyond the scope of the present experiment, as the mix of two PWP types potentially added some noise in the results. Nevertheless, the proposed interpretations seem compatible with a difficulty to adjust the lexical selection threshold in participants with LIFG lesions, which has been suggested so far only for semantic interference in the BCNP (Anders et al., 2017). In a low competitive context (i.e. associative condition of the facilitative PWP type), an unstable lexical selection threshold could not restrain activation spreading unfiltered by competition. Note that functional magnetic resonance imaging studies also pointed out the involvement of the LIFG in semantic processing in speech perception, although its specific role remained largely unclear (see Bookheimer, 2002, for a review).

Before further discussing these results, we will determine if the lesion site (LIFG vs LMTG) also generates differential facilitation effects in another semantically controlled naming paradigm or if they are contingent to the PWP. In Experiment 2, different groups of aphasic participants with lesioned LIFG or LMTG and a group of unimpaired controls underwent the BCNP.

3. Experiment 2: BCNP

Even if the PWP has been very intensively used to investigate word production, the processing of a written or auditory word alongside the picture adds probably a mix of perceptual inputs influencing the time-course of speech planning (Bürki, 2017) and engaging a certain amount of self-monitoring (Dhooge and Hartsuiker, 2012). Therefore, the second experiment was conducted with the BCNP, in which only the presentation of pictures is used, without words.

3.1. Methods

3.1.1. Participants

Twenty aphasic persons were recruited in the University Hospitals of Bordeaux (France) and Lausanne (Switzerland) for this experiment. Seven of them were excluded because of lesions encompassing both the LIFG and the LMTG, or neither area (see Table 4 for the remaining thirteen participants). They previously gave written informed consent validated by local ethical research committees[7] in accordance with the Declaration of Helsinki. They were included if they were French-speaking, right-handed, suffered a first episode of left hemispheric stroke (without prior dementia or psychiatric diseases) and classified as "aphasic" in the first days after the brain damage. All participants were tested three or six months after their stroke, that remained the sole neurologic event at the date of testing. The French version of the BDAE (Mazaux and Orgogozo, 1982) indicated mild anomia in the picture naming subtest and the PPTT (Howard and Patterson, 1992) spared to mildly impaired lexical-semantic knowledge (see Table 4). In the acute phase, all participants underwent clinical brain magnetic resonance imaging (MRI) in Bordeaux University Hospital or in Lausanne University Hospital, except for two participants who underwent computerized tomography (CT) scan. The lesion mapping was conducted as in Experiment 1, and participants were again separated in two groups according to the presence of a lesion in the LIFG with spared LMTG or a lesion in the LMTG with spared LIFG (Fig. 3). The two subgroups of aphasic speakers with damaged LIFG vs LMTG were comparable in terms of age, lesion size and behavioral measures (Table 4).

Table 4
Demographic, lesion and PPTT data of the 13 aphasic persons of Experiment 2.

	Participant	Gender	Age	Lesion size	PPTT
Damaged LIFG	1	male	65	14.96	98%
	2	male	50	30.94	94%
	3	male	66	74.11	87%
	4	male	66	38.52	94%
	5	male	72	71.59	77%
	6	male	55	50.88	98%
	Mean		*62*	*46.83*	*91%*
Damaged LMTG	7	female	78	43.53	92%
	8	male	71	54.38	90%
	9	female	67	100.06	92%
	10	male	67	57.43	90%
	11	male	66	17.8	87%
	12	male	41	7.59	87%
	13	female	52	20.74	98%
	Mean		*63*	*43.08*	*91%*
	p		*.89*	*.81*	*.91*

Damaged LIFG = participants with brain damage encompassing the left inferior frontal gyrus but sparing the left middle temporal gyrus; Damaged LMTG = participants with brain damage encompassing the left middle temporal gyrus but sparing the left inferior frontal gyrus; Lesion size is given in cubic centimeter; PPTT = accuracy at the Pyramids and Palm Trees Test – 3 written words version (n = 52); Means are provided for each subgroup and p-values (Student's *t*-tests) attest that there is no difference between the subgroups.

In addition, thirteen French-speaking and right-handed participants without history of neurological or psychiatric disorder also performed the experiment. This group of unimpaired controls was matched to the group of aphasic participants in terms of sex (three females), age (mean 61.9 y.o., range 41–81) and years of education (mean 14.2 years vs 13.2 years for the brain-damaged group (p = .15)).

3.1.2. Material and procedure

Sixteen items from four non-living categories (furniture, music instruments, tableware, vehicles) and sixteen items from four living categories (animals, body parts, fruit, vegetables) were selected in a large database consisting of color photographs on a white background (Brodeur et al., 2012, 2010; Guérard et al., 2015, see Supplementary Table S2 for the entire list of stimuli). The four chosen items in each category were generally cited in a semantic verbal fluency task (Bueno and Megherbi, 2009) and beginning with different phonemes. The

[7] CPP-SOOM3 in France and CER of Canton de Vaud in Switzerland.

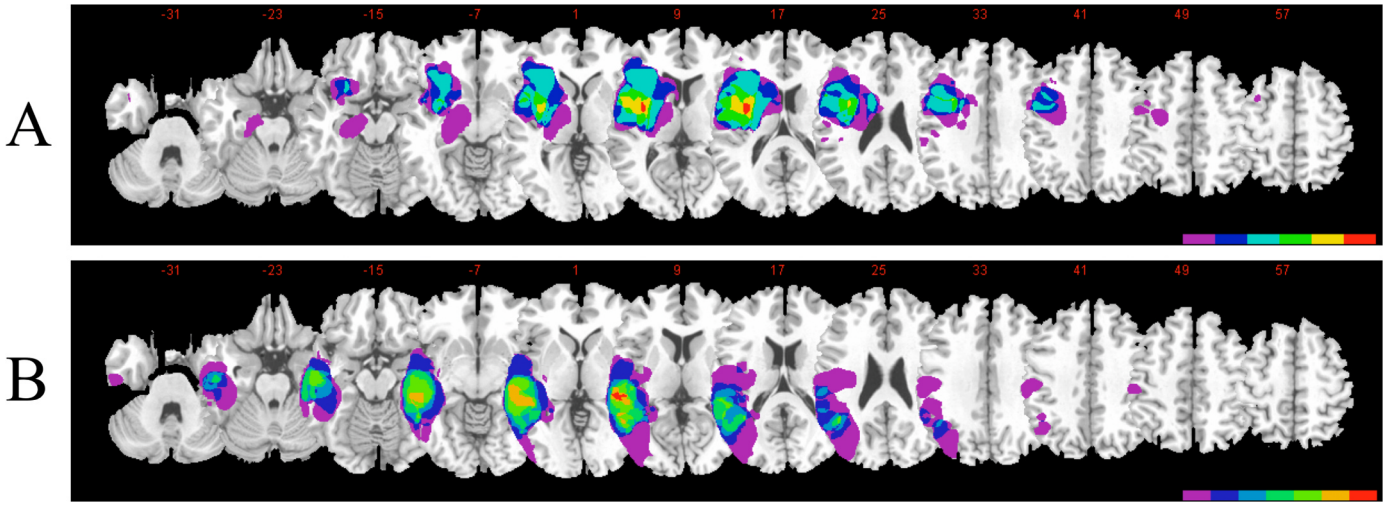

Fig. 3. A. Lesion overlap for the subgroup of six participants with damaged LIFG and spared LMTG; B. Lesion overlap for the subgroup of seven participants with damaged LMTG and spared LIFG.

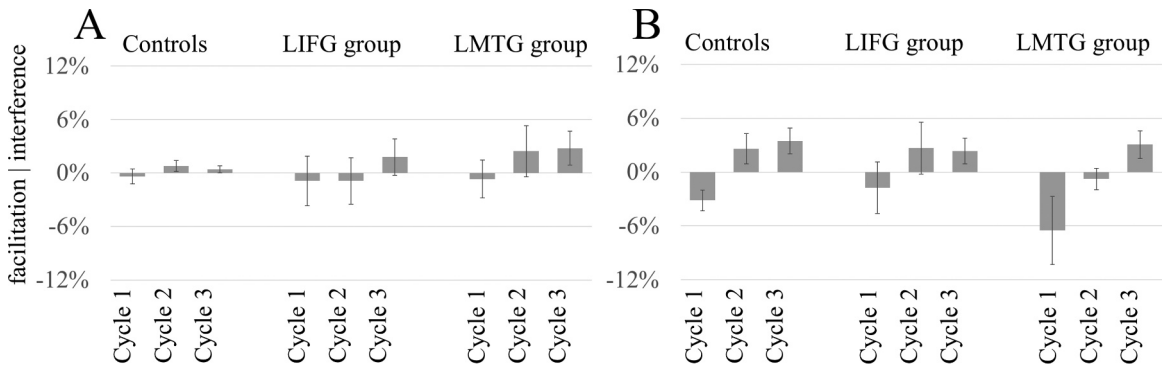

Fig. 4. Mean differences of error rate (A) and proportion of RT differences (B) with standard errors between homogeneous and heterogeneous blocks per cycle for each group of participants; positive values indicate semantic interference and negative values semantic facilitation.

entire set of pictures except one had a high name agreement in the Bank of Standardized Stimuli (above 65%). Each target picture was repeated in three cycles in two different types of blocks (semantically homogeneous vs heterogeneous), so that every subject named each picture six times throughout the experiment, for a total of one hundred and ninety-two trials. Half of the items were first named in homogeneous blocks and the other half first in heterogeneous blocks, to control for a block order effect (Abdel Rahman and Melinger, 2007). The blocks of items were also counterbalanced across participants so that the same items did not always appear first in heterogeneous vs homogeneous blocks. Pictures were presented pseudo-randomly, so that the same target pictures were separated by at least one other picture in two consecutive cycles.

The setting of familiarization and training was the same as in Experiment 1, as well as the hardware and software. In the experimental task, participants were asked to name the pictures as quickly and accurately as possible, which were presented during 1500 ms in the center of the computer screen (responses recorded up to three seconds). A blank screen was then presented for 1500 ms and a green fixation plus sign for 1000 ms before the next picture. The experiment lasted approximately twenty minutes in total, with a fixed break every forty-eight items or flexible breaks on demand.

3.1.3. Analyses

Error scoring, RT extraction and analyses were conducted exactly like in Experiment 1, but the PWP type was replaced by the cycle (as an ordered factor) in the fixed factors alongside the semantic condition (i.e. the type of block: heterogeneous vs homogeneous). Random slopes for the type of block by participants and items were initially included, but not random slopes for the cycle by participants and/or items, because this too complex model failed to converge.

3.2. Results

3.2.1. Global pattern on errors and RTs

Each group of participants displayed the classical differences between the types of blocks both on errors and on RTs (Fig. 4): descriptively, semantic facilitation appeared in the first cycle, whereas semantic interference was observed in later cycles (Table 5).

3.2.2. Accuracy

The mean error rate was 1.6% in the control group (range 0–5.7%), 12.3% in the LIFG group (1.6–34.4%) and 13.2% in the LMTG group (0.5–45.8%), leading to 7.2% of data exclusion due to errors (358 trials among the 4992 observations). Overall, controls were more accurate than the LIFG group ($p = .05$) and the LMTG group ($p = .04$), but no other single variable or interaction reached significance (see Table 6). Errors were essentially semantic errors (25%), hesitations (21%), phonological errors (20%) and omissions (14%). The supplementary analysis for the main error type[8] revealed that the amount of semantic

[8] In order to correct the model for FWE, results were considered significant only when $p \leq .025$ (i.e. $p < .05$ divided by two models conducted on RTs), according to the conservative Bonferroni correction procedure.

Table 5
Mean RT (in ms), overall error rate (in %) and amount of semantic errors (in %) per type of block in each cycle for each group.

		Controls (n = 13)			Damaged LIFG (n = 6)			Damaged LMTG (n = 7)		
		RT	*Errors*	*Sem*	*RT*	*Errors*	*Sem*	*RT*	*Errors*	*Sem*
Cycle 1	HOM	740	2.9%	1.4%	820	16.1%	5.2%	910	18.8%	4.5%
	HET	765	3.8%	1.4%	835	17.7%	2.6%	973	23.7%	5.4%
Cycle 2	HOM	720	2.4%	1.0%	789	14.1%	3.6%	853	18.8%	8.9%
	HET	702	0.2%	0.2%	768	13.5%	4.2%	859	14.3%	1.3%
Cycle 3	HOM	717	1.4%	1.0%	779	11.5%	4.7%	840	17.9%	8.9%
	HET	693	0.5%	0.0%	761	9.4%	0.5%	815	11.6%	1.3%

HOM = homogeneous blocks of stimuli; HET = heterogeneous blocks of stimuli; Sem = semantic errors.

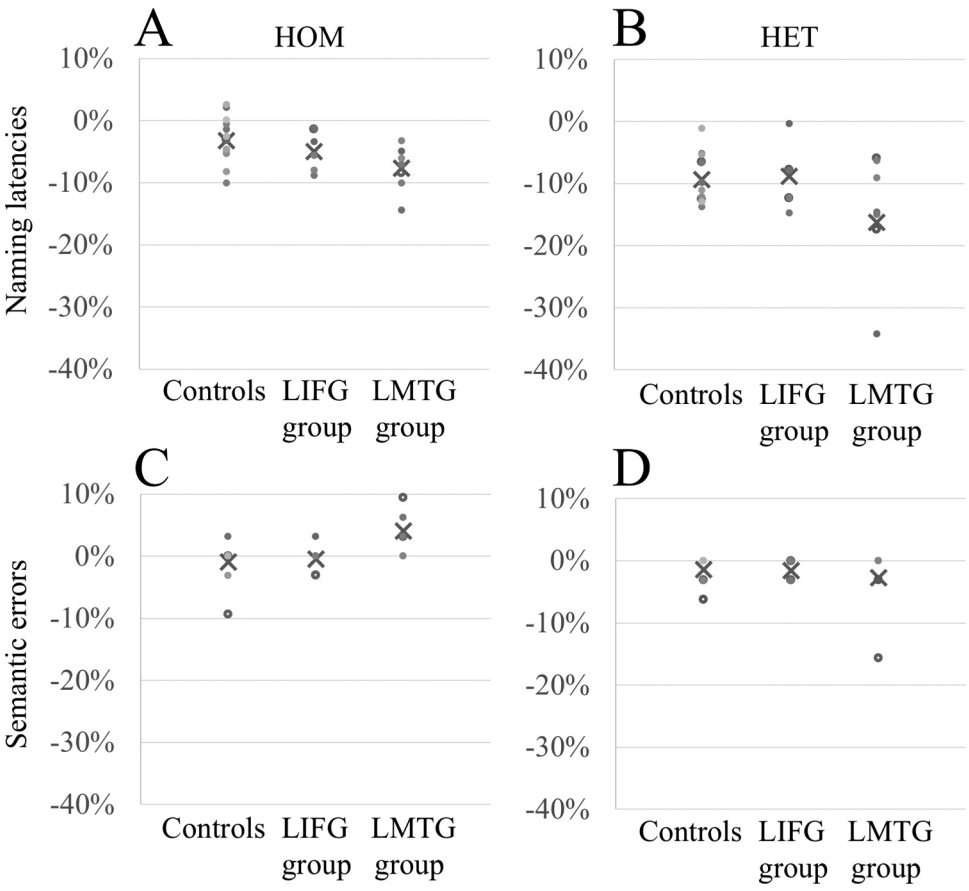

Fig. 5. Behavioral differences in each group of participants between the first and the third cycle: A. Proportion of RT differences in homogeneous blocks; B. Proportion of RT differences in heterogeneous blocks; C. Semantic error rate differences in homogeneous blocks; D. Semantic error rate differences in heterogeneous blocks; crosses represent mean RT differences for each group and dots represent the individual data; negative values indicate facilitation, positive values interference.

errors did not decrease across the cycles in participants with LMTG damage, in contrast to the controls ($p = .02$; see Fig. 5 for the individual data on semantic errors and Table 6 for the full models).

3.2.3. Naming latencies

The exclusion of RTs below/above three standard deviations of each subject's mean concerned 1.7% of responses (84 trials among the 4992 observations) and more precisely 1.8% for the controls, 2.0% for the LIFG group and 1.2% for the LMTG group. The linear regression mixed-effects model on RTs showed main effects of the type of block ($F(1,202.1 = 18.538)$, $p < .001$), of the cycle ($F(1,4391.4) = 211.25$, $p < .001$) and of the group ($F(2,26.6) = 11.713$, $p < .001$) with LMTG participants being overall slower than controls ($p < .001$), whereas the RT differences between LIFG participants and controls did not reach significance ($p = .06$). There were interactions between the type of block and the cycle ($F(1,4388.8) = 30.557$, $p < .001$), and between the cycle and the group ($F(2,4390.3\ 10.271$, $p < .001$). More precisely, only the naming latencies of participants with LMTG damage were dependent of the cycle ($p = .005$), in contrary to the LIFG group who did not differ from controls in this respect (see Fig. 5 for the amount of repetition priming in both types of blocks for the three groups). Across the cycles, participants with LMTG damage thus showed more repetition priming on naming latencies than the control participants. To check if the main interaction between the cycle and the group was only due to certain participants, another model was computed with random slopes for the cycle by participants and by items (instead of the type of block in the initial model), and the interaction remained significant ($F(2,23.3) = 3.328$, $p = .05$).

As in Experiment 1, we checked whether the lesion size correlated with the differences between semantic conditions in terms of naming latencies or errors, which does not seem to be the case (all Spearman coefficients between -0.25 and 0.39 all $ps > .05$).

Table 6
Results of the inferential statistics for the error rates (top), the semantic errors (mid) and the naming latencies (bottom) in the BCNP.

Effects on errors	β	SE	z	p	
HOM vs HET	1.969	1.369	1.438	0.150	
Cycle	− 0.394	0.371	− 1.063	0.288	
LIFG vs controls	1.925	0.993	1.939	0.053	
LMTG vs controls	1.997	0.962	2.076	0.038	
HOM vs HET : cycle	− 1.810	1.041	− 1.739	0.082	
HOM vs HET : LIFG vs controls	− 1.629	1.468	− 1.110	0.267	
HOM vs HET : LMTG vs controls	− 1.621	1.451	− 1.117	0.264	
Cycle : LIFG vs controls	0.325	0.415	0.782	0.434	
Cycle : LMTG vs controls	0.311	0.406	0.765	0.444	
HOM vs HET : Cycle : LIFG vs controls	1.594	1.074	1.484	0.138	
HOM vs HET : Cycle : LMTG vs controls	1.478	1.069	1.382	0.167	
Effects on semantic errors	β	SE	z	p	
HOM vs HET	1.531	1.418	1.080	0.280	
Cycle	− 0.665	0.435	− 1.529	0.126	
LIFG vs controls	0.674	1.146	0.588	0.557	
LMTG vs controls	− 0.137	1.104	− 0.124	0.901	
HOM vs HET : cycle	− 1.427	1.070	− 1.334	0.182	
HOM vs HET : LIFG vs controls	− 1.607	1.719	− 0.935	0.350	
HOM vs HET : LMTG vs controls	− 0.258	1.720	− 0.150	0.881	
Cycle : LIFG vs controls	0.586	0.518	1.132	0.258	
Cycle : LMTG vs controls	1.117	0.492	2.274	0.023	
HOM vs HET : cycle : LIFG vs controls	1.050	1.177	0.893	0.372	
HOM vs HET : cycle : LMTG vs controls	− 0.193	1.211	− 0.159	0.874	
Effects on naming latencies	β	SE	df	t	p
HOM vs HET	0.062	0.019	178	3.137	0.002
Cycle	− 0.015	0.005	4382	− 2.721	0.007
LIFG vs controls	0.118	0.061	29	1.942	0.062
LMTG vs controls	0.237	0.058	29	4.108	< 0.001
HOM vs HET : cycle	− 0.034	0.008	4383	− 4.422	< 0.001
HOM vs HET : LIFG vs controls	− 0.016	0.036	202	− 0.454	0.651
HOM vs HET : LMTG vs controls	0.032	0.034	199	0.951	0.343
Cycle : LIFG vs controls	− 0.011	0.010	4386	− 1.064	0.287
Cycle : LMTG vs controls	− 0.027	0.010	4389	− 2.803	0.005
HOM vs HET : cycle : LIFG vs controls	0.009	0.014	4385	0.602	0.547
HOM vs HET : cycle : LMTG vs controls	− 0.007	0.014	4387	− 0.536	0.592

HOM = homogeneous blocks of stimuli; HET = heterogeneous blocks of stimuli; LIFG = group of six participants with a lesion in the left inferior frontal gyrus; LMTG = group of seven participants with a lesion in the left middle temporal gyrus; controls = control group of thirteen unimpaired participants.

3.3. Discussion

3.3.1. Semantic facilitation and interference in the BCNP

The semantic manipulation of the BCNP (homogeneous vs heterogeneous blocks) did not allow to distinguish the result pattern of the three groups of participants: both controls and brain-damaged (LIFG and LMTG) speakers showed the classical reversal of semantic facilitation turning into interference. In comparison with previous BCNP studies, we did not find semantic interference on accuracy increasing over the cycles in patients with frontal lesions, probably because we targeted the investigation of facilitation effects and used only three cycles, as compared to other studies running more cycles to maximize interference effects (e.g. six cycles in Riès et al., 2015; eight cycles in Harvey and Schnur, 2015). Note also that the error rate was lower in the present sample of individuals with LIFG lesions (on average 9.4–23.7%) than in other studies (e.g. 17–33% in Riès et al., 2015).

3.3.2. Repetition priming in the BCNP

Repetition priming on naming latencies over the cycles (independently of the semantic condition) was significantly larger in individuals with a LMTG lesion as compared to unimpaired individuals, whereas the LIFG group behaved similarly to controls. In contrast to repetition priming effects on latencies, the occurrence of semantic errors did not decrease across the cycles in participants with LMTG damage, while controls and the LIFG group benefited from the repetition of the same pictures on both accuracy and speed. Repetition priming refers to better processing when retrieving a picture name that has been previously produced even after up to 100 intervened trials (Wheeldon and Monsell, 1992). This facilitative long-lasting effect necessarily implies that some resting activation of previously named items remains latent or slowly declines, in such a way that subsequent retrievals of the same words are speeded up. Repetition priming is typically the result of strengthened connection weights of semantic-to-lexical mapping (Oppenheim et al., 2010) or between semantic features (Wheeldon and Monsell, 1992). In that sense, it is rather associated with pre-lexical processes.

3.3.3. The LMTG contribution

Due to the specific pattern of repetition priming in patients with LMTG lesions, this area seems related to pre-lexical processes and might play a role in properly mapping semantic concepts to their lexical labels in word production. Actually, the LMTG is thought to blur the fine-grained feature distinctions conveyed by semantic-to-lexical connections (Schwartz et al., 2009) and to be critical to understand the meaning of single words (Dronkers et al., 2004). The dark side of a dysfunctional concept-to-word mapping might result in the production of semantic errors (as in Schwartz et al., 2009), but it might come with a brighter side when word production is successful (i.e. without errors) resulting in magnified repetition priming. The interpretation of impaired pre-lexical processes after a LMTG lesion, for instance because of residual activation not decaying as quickly as it should, could explain both the stable occurrence of semantic errors, as well as increased repetition priming effects on naming latencies. Hence, a LMTG lesion could disturb a learning algorithm (Schwartz et al., 2009) or booster

mechanism (Oppenheim et al., 2010) related to semantic-to-lexical mapping. As a consequence, both sides of incremental learning might become dysfunctional (see Oppenheim et al., 2010, for a description of these light vs dark sides): the lack of semantic error reduction might be due to the (exacerbated) dark side of weakening semantic-to-lexical connections to competitors, whereas the exaggerated facilitation effects on naming latencies to the (exacerbated) light side of strengthening semantic-to-lexical connections.

4. General discussion

In contrast with the majority of previous studies conducted on aphasic speakers, we analyzed both facilitation and interference in two paradigms generally used to investigate lexical-semantic processes, the PWP and BCNP. Also, our main results and interpretations concerned naming latencies and not speech errors. Even if the study of errors has a long tradition in aphasia research and offers a nice opportunity to understand how word production is affected by a brain lesion, it is not unanimously accepted as a valid measure to inform on "normal" speech production, where careful measurements of naming latencies might be considered as more appropriate (Dell et al., 2014). Individuals with damaged LIFG showed exaggerated semantic facilitation in the PWP with long SOAs as compared to controls (Experiment 1), whereas individuals with damaged LMTG displayed exaggerated facilitation by repetition priming on naming latencies, but no repetition priming on semantic errors in the BCNP as compared to controls (Experiment 2). Importantly, the exacerbated facilitation effects described here do not mean that brain-damaged speakers were faster than unimpaired controls to name pictures (they were indeed overall slower), but it reveals an increased sensitivity to the experimental context, namely semantic primes in Experiment 1 for the LIFG group and repetition of items in Experiment 2 for the LMTG group. These dissociations allow attractive insights to the mechanisms and brain areas involved in word production. The LMTG seems to convey semantic-to-lexical connections that are closely influenced by repetition/learning. A lesion encompassing the LMTG might inadequately affect the connections weights between the concepts and their lexical representations, increasing repetition priming but also making the semantic-to-lexical process error-prone. This interpretation of the LMTG contribution (based here on repetition priming on RT patterns without facilitation on semantic errors in the BCNP) is consistent with error data previously reported in the PWP, namely increased interference after categorical words (e.g. cow-pig) as compared to unrelated words (e.g. chair-pig) but also increased incongruency effects (i.e. more errors after unrelated words than after congruent words, e.g. pig-pig) in participants with LMTG lesions (Piai and Knight, 2017), which we did not find here because of the low error rate and methodological differences (long SOA, associative vs congruent words). As for the LIFG, it seems to participate to the adjustment of the lexical selection threshold. A lesion encompassing the LIFG might deregulate the spread of activation in the lexical network intermittently overriding lexical competition (Anders et al., 2017; Schnur et al., 2006), and might result in the reliance on compensatory strategic processes (e.g. over-reliance on the cues provided). This interpretation of the LIFG contribution (based on RT patterns in the PWP in the present case) is consistent with error data previously reported in the BCNP, namely semantic interference increasing over the cycles in participants with LPFC lesions (Riès et al., 2015), which we did not find here because of the low error rate and methodological differences (low number of cycles and inclusion of the first cycle in the analyses).

The present data and interpretations are in line with models locating semantic-lexical activation in the left temporal lobe and competitive lexical selection in the left inferior frontal lobe. It is in harmony with the anatomical model synthesizing 20 years of PET/fMRI studies (Price, 2012) concluding that the semantic-to-lexical mapping involves the left temporal lobe (middle and postero-inferior parts), whereas lexical selection among competitors rather takes place in the frontal lobe (middle and superior parts).

Although twenty-five brain-damaged individuals were tested in the current study, this remains a small size sample and lack of statistical power might be a possible issue, especially when looking at subgroups of six aphasic speakers not behaving as homogeneously as healthy speakers. Moreover, different participants were tested in Experiment 1 (n = 12) and in Experiment 2 (n = 13), and these subgroups differed regarding the chronicity of aphasia. For these reasons, a direct between-experiment comparison cannot be made without caution. Given the uniqueness of each brain, lesion size and location, fine-grained spatial localization of the precise structures concerned (such as Brodmann areas or white matter tracts) is beyond the scope of the current study, that rather complements functional neuroimaging studies to define in which aspect of word production the LIFG and the LMTG are mainly involved.

5. Conclusion

The increase of semantic facilitation in participants with damaged LIFG in the PWP provides crucial information about the role of this region in word production. It seems an essential area to regulate automatic spreading activation/inhibition to candidates/competitors within the lexical network, which is probably compensated by more controlled processes after a LIFG lesion. The stagnation of semantic errors and the increase of repetition priming on production speed across the cycles of the BCNP in participants with damaged LMTG indicates that the mapping from semantics/concepts to words shall be conveyed in this region. The increased sensitivity to facilitation by the semantic context and by repetition reported here in groups of aphasic speakers offer new perspectives for the investigation of facilitation effects in brain-damaged individuals, that seem as informative as semantic interference to inform on word production processes.

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Declaration of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neuropsychologia.2018.10.026.

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